Vegetation structure and decreased moth abundance limit the recolonisation of restored habitat by the European Nightjar

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Abstract

Woodland ecosystems of Europe have undergone major transitions in the last centuries. Changes in land use and the loss of natural forest dynamics have often led to structurally poor, uniform and dense stands. Not surprisingly, open forest species relying on a heterogeneous stand structure have suffered dramatic population declines. The European Nightjar *Caprimulgus europaeus*, a nocturnal insectivorous bird, has undergone such a decline in its main Swiss stronghold in Valais. Despite the species' potential to colonize new sites and habitat restoration measures implemented since 2001, recolonisation of restored sites has not taken place, suggesting problems with the current habitat restoration strategy. In order to refine management recommendations, we compared habitat structure and moth abundance, a key Nightjar food source, at sites that are still occupied and at sites that had been abandoned but have recently been restored. Vegetation structure was more heterogeneous and moth abundance greater at occupied than at abandoned sites. More specifically, occupied sites harboured a greater coverage of bare ground, while abandoned sites exhibited a higher amount of regeneration and intermediate shrub layer. The occurrence of natural perches was also higher in occupied sites. Abandoned sites are thus characterised by lower prey abundance and denser vegetation cover, the combination of which is likely to lead to lower prey availability for hunting Nightjars. Restoration action would benefit from maintaining snags and dead branches and by targeting unproductive habitats characterised by mineral soils, thereby slowing down regeneration and shrub regrowth. For future successful management of Nightjar habitats, it seems thereby essential trying to find the balance between actions that allow opening the lower and mid-strata of the forest while sustaining high moth populations.

Introduction

European forest ecosystems have undergone substantial changes over the last few centuries (Nilsson 1997; McGrath et al. 2015). After strong declines following the expansion of agriculture, the forested area has started to recover since the beginning of the 20th century. The changes in timber harvesting practices have led to a homogenisation of forest structures, which can have negative effects on biodiversity (Spiecker 2003). Awareness of the importance of sustainable forest management for biodiversity and ecosystem services only emerged within the last 20 years (e.g. Lähde, Laiho and Norokorpi 1999; Bengtsson et al. 2000; Führer 2000; Seymour et al. 2002). Natural hazards and disturbances are important drivers of natural forest ecosystems (Angelstam 1998; Kuuluvainen 2009; Kulakowski et al. 2011): they create pioneer habitats whose natural successional stages harbour locally adapted faunal and floral communities (Angelstam 1998). Although some forest species might benefit from stand homogenisation (Paillet et al. 2009; Fonderflick et al. 2010), pioneer species will suffer, notably those depending on the early stages of the vegetation succession.

The European Nightjar, *Caprimulgus europaeus*, is a nocturnal bird species and is mostly relying on open habitats in wooded areas. With the loss of heathlands in Great Britain, previously the main habitat for Nightjars (Conway et al. 2007), other wooded habitats became more important such as young coniferous forest plantations (Sharps et al. 2015), clear fells up to 10 years after tree plantation (Cross et al. 2005) or forested sites after the occurrence of a major disturbance (Scott et al. 1998). This selection for younger growth reflects a preference for semi-open habitats, where a subsequent tree regrowth of up to 2–3 meters results in an unsuitable habitat (Ravenscroft 1989). A study in an inner-alpine valley in Switzerland similarly revealed a positive effect of semi-open landscapes (mainly oak-pine scrublands) where Nightjars preferred habitats with 20–50% tree coverage (Sierro et al. 2001). The requirement of a fairly open habitat is associated with the hunting strategy of the Nightjar. Nightjars spot their flying prey, mostly moths (Glutz von Blotzheim and Bauer 1994), from the ground or a perch, discriminating them from the sky background (Jackson 2003). They prefer catching their prey from below (Glutz von Blotzheim and Bauer 1994) and hence need open space to be able to follow their prey. Recent studies indicate that Nightjars show a certain degree of plasticity in spatial foraging behaviour (Evens et al. 2017, Sharps et al. 2015). In order to reach optimal feeding grounds birds can travel long distances, which is however physiologically costly (Evens et al. 2018).

While the European Nightjar is categorized as least concern by the IUCN (Bird-Life International 2012), the species is of conservation concern in Switzerland (Keller et al. 2010), with roughly 80% of the Swiss population occurring in the southwest

(Valais). Over the past five decades this Nightjar population has steadily declined, with the abandonment of several sites and the colonisation of only a few major new sites created by forest fires (Sierro 2013). This decline might partly be associated with habitat degradation by changes in land use and forest management (Langston et al. 2007) that may affect the optimal vegetation structure and/or the abundance of prey, i.e. large moth species (Jackson 2003, Sierro et al. 2001). In effect, the majority of Valais forests were progressively transformed into denser stands (Bollmann et al. 2009), which represent unsuitable habitats for an open habitat species such as the Nightjar. Several targeted habitat restoration measures, based on evidence from the UK (Morris, Burges and Fuller 1994; Cross et al. 2005) and central Europe (Sierro et al. 2001; Wichmann 2004) have been implemented at 18 abandoned sites in Valais since 2001. Measures included varying sizes of clear-cuts (up to 2 ha), selective logging and habitat maintenance via grazing by highland cattle and goats (Sierro 2013). Despite a long term Nightjar monitoring scheme (Sierro 2013), only scarce observations of displaying males in seemingly restored habitats could be gathered. This, despite the fact that Nightjars in Valais are able to recolonize new sites as shown in a burnt woodland site where several individuals colonized the area a few years after the fire. Overall, this suggests that the locally implemented Nightjar restoration programme was not properly targeting the species-specific ecological requirements of the Nightjar.

In this study, we analyse variation in vegetation structure in the southwestern part of Switzerland, as well as the abundance, biomass, species richness and diversity of moths in abandoned and restored sites and compare them to sites occupied by the European Nightjar. Vegetation structure was investigated to identify fine-scale habitat preferences of the Nightjar while data on moth abundance and diversity should highlight whether local prey could be a limiting factor in abandoned sites. Based on these findings, we shall provide new, refined management recommendations to hopefully improve restoration actions.

Materials and methods

Study area and model species

The study was conducted in Switzerland in the canton of Valais between Martigny (Les Follatères: 46°07'25.71N, 7°04'30.90E) and Visp (Ausserberg: 46°19'31.03N, 7°50'47.98E) in the upper Rhône valley. The habitats of the Nightjar within this inner-alpine valley are characterized by a continental climate with a low amount of precipitation throughout the year (~ 550–700 mm/year), cool winters and warm to hot summers. Study sites were located between 570 and 1500 m a.s.l. Occurrence data for the European Nightjar were obtained from a monitoring programme of the species in the canton of Valais starting in 2000 (Sierro 2000; Sierro 2013), and from random observations of accredited contributors of the Swiss Ornithological Institute. Occupied sites

were defined as having had at least one singing individual in the year 2012, and sites that were regularly occupied in the last six years (2007–2012). The location of a singing male is a valid spatial indicator of an occupied territory of a paired male (Schlegel 1967) or of a solitary male that can move between vacant territories (G. Conway, pers. comm.). In both cases, the location of a singing male is expected to reflect current potential breeding habitat. In contrast, abandoned sites lacked observations between 2002 and 2012 but had regular observations between 1980 and 2002. Using these criteria, we selected 22 abandoned and 13 occupied sites. In all abandoned and two occupied sites (see Suppl. material: SI1), various habitat restoration measures, ranging from clear-cuts to grazing, were implemented in the last decade (2001–2011).

Vegetation structure

For all 35 sites we estimated the vegetation structure at the site of the light trap (for details see 'Moth sampling and identification') and on randomly selected vegetation survey locations, defined as points (function 'Random Point Tool' in QGis 1.7.4, QGIS Development Team 2013) in September and October 2013. The number of sampling points was adjusted to the size of the site, resulting in one to six points per site. If a sampling point was close the forest edge, its centre was moved to ensure that only the clear-cut was sampled and not the adjacent forest. Habitat variables were estimated at two different scales. Fine-scaled habitat characteristics were estimated on a 10 × 10 m square plot and larger structures on a circular plot with a 15 m radius. Each 10 × 10 m plot was further divided into four equal squares (5 × 5 m) in order to ensure the correct mapping of the mean height and the percentage cover of ground vegetation (grass and herbs), the percentage cover of bare ground (including the sum of litter, soil, sand, gravel, stones, and rock; Table 1) and the amount of lying dead wood. The mean of the 5 × 5 m squares was used for further analyses. On the 15m-radius circular plot, we counted the number of perches (standing dead wood; higher than 1 m and greater than 10 cm in diameter) and estimated the overall coverage, of the regeneration (<1.3 m), shrub (1.3–5 m) and tree layer (>5 m) (see Table 1 for details). Given that the status (occupied, abandoned) of each site was known, we tried to avoid any potential bias in the estimated habitat variables by always having two observers estimating habitat characteristics.

Moth sampling and identification

Within all 35 sites, moths were sampled on a random spot (QGis 1.7.4, QGIS Development Team 2013) at least 20 m from the forest edge to avoid sampling bias due to vegetation structure. We sampled for four hours starting at sunset under good weather condition (15.6 ± 3.3 °C (mean±SD), no precipitation) and around the new moon. Moths were sampled using an automatic light trap with a 12-W super actinic bulb (Bioform Entomology & Equipment, Nürnberg) powered with 12-V lead-acid batter-

Table 1. Vegetation data were assessed on all occupied and abandoned sites of the European Nightjar in southwestern Switzerland. Ground vegetation and bare ground variables were estimated on a 10 × 10 m plot (mean of four 5 × 5 m plots). On the 15 m-radius plot we counted the number of perches and estimated several vegetation layers on different heights.

Scale	Variable	Description	Unit
10×10	Ground vegetation cover	Cover of herbs and grasses	%
	Groud vegetation height	Mean height of herbs and grasses	cm
	Bare ground	Cover of rocks, stones, gravel, sand, soil and litter	%
	Lying dead wood	> 1.3 m, > 10 cm Ø	Quantity
15 m radius	Perches (standing dead trees)	>1.3 m, >10 cm Ø	Quantity
	Tree layer	> 5 m height	%
	Shrub layer	>1.3, < 5 m	%
	Regeneration layer	< 1.3 m	%

ies. Collecting bottles below the light trap were partly filled with ethyl acetate to store moths upon capture. Each trap was emptied the following day and moths were stored in a plastic bag, while the ethyl acetate was removed. Samples were frozen for later identification at -18 °C.

Moths were sampled in May (7–12), June (8–15) and July (3–11) 2013 with a single light trap per site, where eight traps were randomly allocated to abandoned and occupied sites each night. This method controls for differences in daily weather conditions (temperature, cloud cover, wind) and phases of the moon (Yela and Holyoak 1997). All sites were sampled in June and July, and 27 sites were sampled in May, resulting in 97 sampling events in total.

Moths were identified to species or morphospecies when possible (Derraik et al. 2002); poorly preserved individuals were only identified to the family level and were treated as one unknown species per family. Since Nightjars mainly feed on larger moths (80% of diet), small Lepidoptera (body length < 0.8 cm) were excluded from the analysis (Schlegel 1967; Sierro et al. 2001). To estimate the dry biomass of captured moths we randomly selected three individuals per species, dried them in an oven at 60 °C for at least 20 h, and kept them at room temperature for at least 4 h before weighing. The mean mass of these three individuals was used to calculate the species' biomass (mg). The mean of all identified species of one moth family was used for the unidentified individuals of this given family.

Statistical analysis

All analyses were performed using the R version 3.0.2. (R Core Team 2013). Differences in vegetation structure variables between occupied and abandoned sites were analysed using the mean of the vegetation sampling points (1 to 6) per site. First, we fitted univariate generalized linear models with a binomial error structure, with occupied/abandoned as a response variable and each vegetation structure element as an explanatory variable. Linear and quadratic terms, using the poly function (orthogo-

nal polynomials), were used to test vegetation variables explaining the occurrence of the Nightjar. Variables contributing significantly to the presence of the Nightjar were tested for multicollinearity (Spearman's $|r_s| \geq 0.7$). No multicollinearity was detected among significant variables. No or weak spatial autocorrelation was observed for these variables using Moran's index (bare ground: I=-0.54, p=0.59; number of perches: I=0.86, p=0.39; regeneration layer: I=2.26, p=0.02 (indicative of clustering); shrub layer: I= p=0.15; tree layer: I=1.05, p=0.29). We then tested all possible combination including the null model to identify the most parsimonious model according to the Akaike information criterion (`dredge` function of the `MuMIn` R-package; Bartoń (2015)). The most competitive models according to the AIC (Δ < 2; Barton 2012) are presented. R^2 was calculated with the rsquare function in the piecewiseSEM package (Lefcheck 2016).

Moth abundance, biomass, species richness and diversity (Shannon index in the vegan package; Oksanen 2013) were analysed in relation to site status (abandoned vs. occupied sites). We used linear mixed effect models with Poisson error distribution for moth abundance and species richness and Gaussian error distribution for moth biomass and diversity. We used abundance, biomass, species richness and diversity of all captured moths as response variables, site status and month as explanatory variables, and site as a random factor.

Results

Vegetation structure

Using univariate approaches, five variables revealed a difference between occupied and abandoned sites (Table 2). At the ground level bare ground showed higher values on occupied than on abandoned sites, indicating some preference for a more open habitat. The amount of perches exhibited a quadratic relationship with Nightjar occurrence, with the lowest and highest amounts of dead wood correlating to a higher probability of occurrence. The regeneration layer (<1.3 m) covered greater percentages within abandoned sites than in occupied sites, indicating that abandoned sites have relatively denser vegetation cover. The shrub layer (1.3–5 m) exhibited a quadratic pattern, with lowest and highest observed amounts of coverage occurring in abandoned sites. The number of perches was significantly higher in occupied sites compared to abandoned sites (Table 2). The density of the tree layer did not differ between occupied and abandoned sites in the univariate models. Moreover, the presence of Nightjar was not correlated to ground vegetation cover (grass and herbs), nor vegetation height could sufficiently explain the observed occurrence patterns of the Nightjar. The most competitive models (Table 3) demonstrate that occupied sites differ from abandoned sites by having a combination of a higher cover of bare ground, a more open regeneration layer, higher values at an intermediate cover of the shrub layer, and a higher number of perches (Fig. 1).

Table 2. Variables of the univariate approach with occupied/abandoned sites as binary response variable. For statistical details see material and methods.

No	Variable	Estimate	SE	z-value	p-value	AIC
1	Intercept	-0.53	0.35	-1.50	0.13	
	Ground vegetation cover	0.21	2.06	0.1	0.92	50.17
2	Intercept	-0.54	0.36	-1.52	0.13	
	Ground vegetation height	-2.13	2.18	-0.98	0.33	49.18
3	Intercept	-0.60	0.38	-1.58	0.11	
	Bare ground	4.57	2.40	1.90	0.057	45.99
4	Intercept	-0.55	0.36	-1.54	0.13	
	Laying dead wood	-2.70	2.22	-1.21	0.23	48.61
5	Intercept	-0.62	0.40	-1.57	0.12	
	Perches	6.23	2.54	2.45	0.01	42.65
6	Intercept	-0.57	0.38	-1.51	0.13	
	Tree layer	5.39	2.77	1.95	0.05	44.99
7	Intercept	-1.01	0.54	-1.87	0.06	
	Shrub layer	-2.43	3.24	-0.75	0.45	
	Shrub layer^2	-10.78	5.25	-2.05	0.04	43.58
8	Intercept	-0.69	0.41	-1.67	0.09	
	Regeneration layer	-7.21	2.93	-2.46	0.01	41.79

Moth abundance, biomass and diversity in relation to site status

A total of 8397 moths were collected, representing 260 different species from 11 families (Arctiidae, 613; Cossidae, 4; Drepanidae, 6; Geometridae, 973; Lasiocampidae, 345; Limacodidae, 13; Lymantriidae, 30; Noctuidae, 6070; Notodontidae, 142; Sphingidae, 191; Thyatiridae, 4; unknown, 6; Suppl. material: SI2, SI3). The fewest moths were sampled in May (1198, N = 27), with a continuous increase in June (2374, N = 35) and July (4825, N = 35). Occupied sites show a higher abundance of moths, dependent of month (interaction site status * month: 32.2 ± 13.11, z = 2.27, p = 0.02; Fig. 2a). This interaction is best explained by an increasing difference of moth abundance within the season. While both months May (20.87 ± 22.2, z = 0.94, p= 0.35) and June (33.93 ± 20.33, z = 1.67, p = 0.1) do not have a higher moth abundance in occupied compared to abandoned sites, this effect is significant in July (84.55 ± 20.33, z = 4.16, p < 0.01). A similar pattern was found when analysing moth biomass (Fig. 2b). Biomass differs among occupied and abandoned sites and within the season (interaction site status * month: 1885.17 ± 642.98, $t_{65.91}$= 2.61, p = 0.01). Again, moth biomass did not differ in May (292 ± 1003.4, $t_{1,33}$ = 0.29, p = 0.78) and June (812.1 ± 909.8, $t_{1,33}$= 1.71, p = 0.1), but biomass was significantly larger in occupied sites in July (3983.49 ± 909.76, $t_{1,33}$= 2.87, p < 0.01).

Moth species richness tended to be higher in occupied sites than in abandoned sites (3.645 ± 1.9, z = 1.91, p = 0.056; interaction site status * month: 1.02 ± 2.12, z = -0.44, p = 0.66; Fig. 3a) while there was no difference in species diversity (-0.01 ± 0.1, t_{95} = -0.06, p = 0.95; interaction site status * month: -0.1 ± 0.12, t_{94} = -0.87,

Table 3. The three most competitive models (ΔAICc <2). The ranking is based on the AIC.

Rank	Included Variables	AICc	ΔAICc	R²
1	Shrub, shrub², regeneration layer	32.8	0	0.49
2	Bare ground, shrub, regeneration layer, perches	33.2	0.42	0.54
3	Shrub, regeneration layer, perches	34.6	1.82	0.45
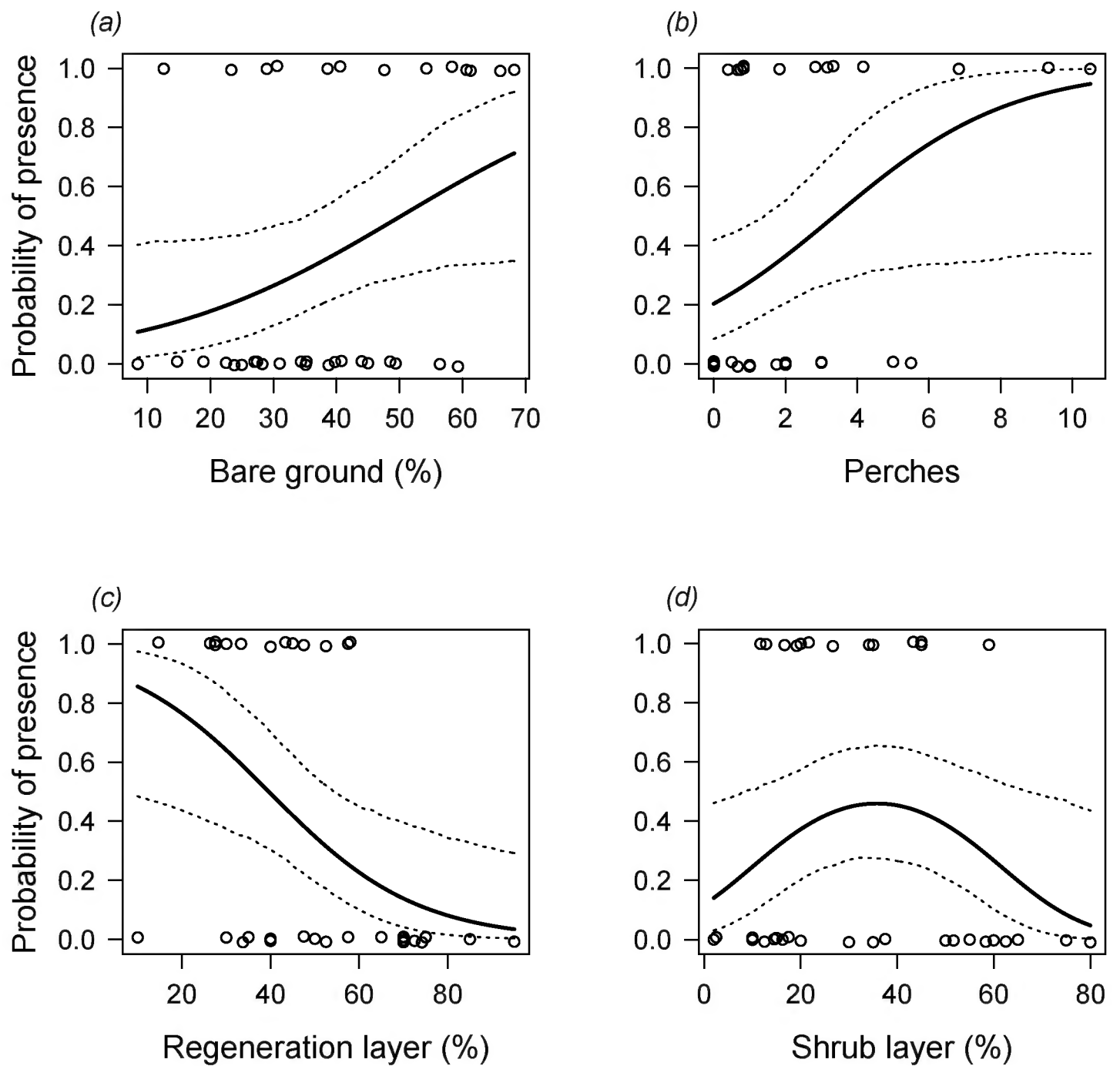
Figure 1. Probability of occurrence of Nightjar in relation to vegetation structure variables appearing in the most competitive models tested: **a** bare ground **b** perches **c** regeneration layer and **d** shrub layer. Vegetation structure variables are shown with regression lines and 95% confidence intervals (dotted lines), open circles = occupied (1) and abandoned (0) jittered in vertical direction.

$p = 0.39$; Fig. 3b). Both species richness and diversity increased from May to July (species richness: 10.61 ± 1.03, $z = 16.45$, p < 0.001; diversity: 0.46 ± 0.06, $t_{96} = 7.97$, p < 0.001).
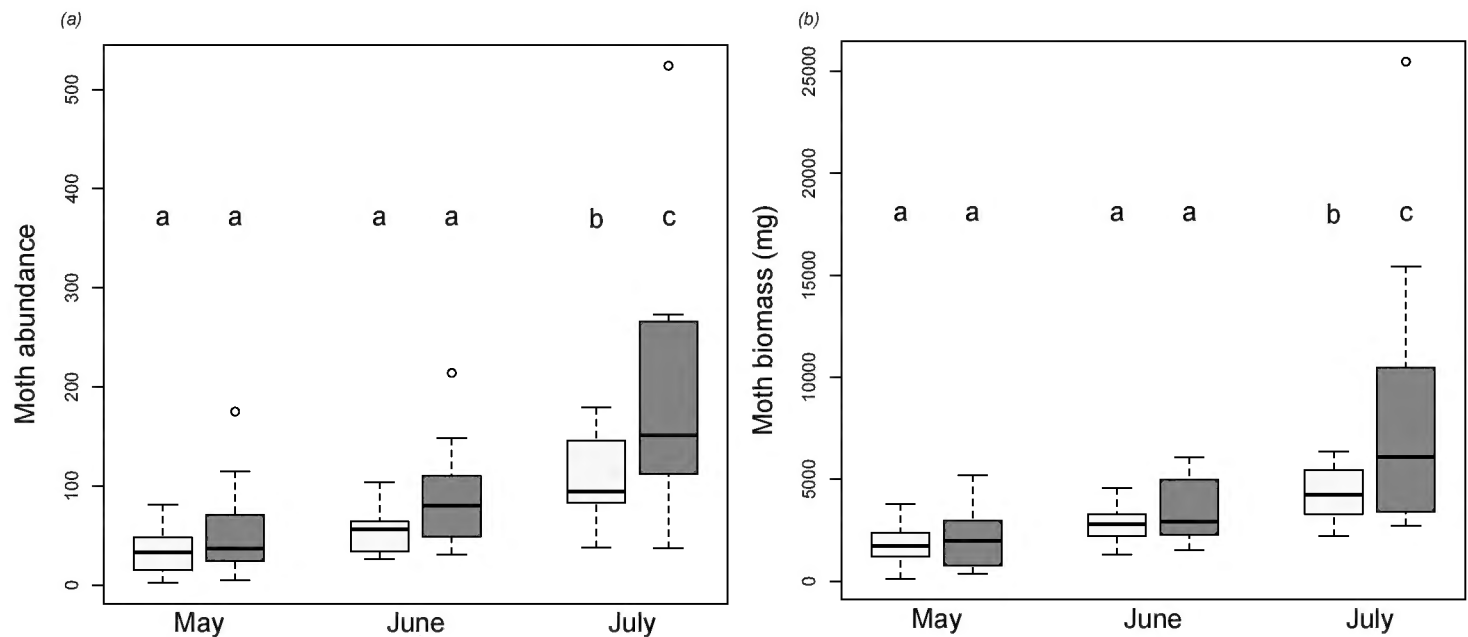
Figure 2. Moth abundance **a** and moth biomass **b** increased in occupied (dark grey) and abandoned sites (light grey) from May to July. The boxplots indicate the 25%, 50% (bold line) and 75% limits of moth biomass, whiskers the 10% and 90% deciles. The open dot indicates an outlier. Statistically significant differences, depicted by different letters on column tops, occurred only in July.
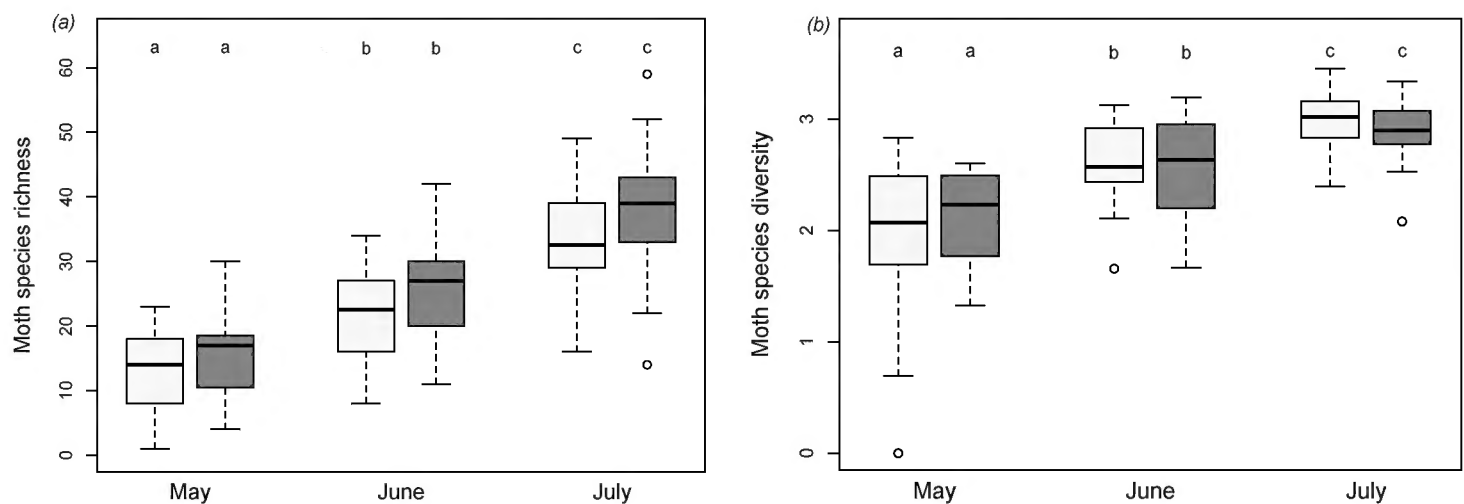

Figure 3. Boxplots of species richness **a** and species diversity **b** in relation to occupied (dark grey) and abandoned sites (light grey) from May to July. Boxplots visualize the 25%, 50% (bold line) and 75% limits where the whiskers indicate the 10% and 90% deciles. Open dots indicate outliers. Different letters depict statistically significant differences.

Discussion

This study establishes that Nightjar occurrence in the upper Rhône valley (SW Switzerland) can be associated with an open vegetation matrix that offers abundant prey (moth) resources. Although our findings cannot disentangle the relative importance of these two factors in explaining the occurrence of the Nightjar, they can help to refine habitat restoration guidelines for this endangered nocturnal bird species.

Vegetation structure differed between abandoned and occupied sites at different height levels. At the ground level, an open habitat seems to be especially important,

as evidenced by the high percentage of bare ground coverage found in occupied sites. Our results contrast with the study by Wichmann (2004) who did not find any such relationship, most likely because the study area consisted of nutrient poor soils across the whole range (Wichmann 2004). The importance of habitat openness at ground level was emphasized by several studies and may be important for nest building (Cross et al. 2005; Verstraeten et al. 2011), egg and chick concealment (Jackson 2003) and to escape approaching predators (Camacho 2014). Alternatively, an open habitat at low levels facilitates the hunting strategy of the Nightjar, which often sits on the ground and spots flying moths that are more easily discriminated in front of a lighter sky background (Jackson 2003). The cause for the open ground in occupied sites may ultimately lie in the stone- and gravel-rich substrate that hinders vegetation regrowth, as typically observed on unproductive soils of floodplains or rocky steppes. The fact that several abandoned, and subsequently rehabilitated sites in our study area were on rather productive soils led to a rapid regrowth after habitat restoration measures, probably rendering the habitat unsuitable for Nightjar already in a short term.

Although several studies have indicated the importance of shrubs for Nightjar (Bartolommei et al. 2013; Sharps et al. 2015), our study refines these findings by demonstrating a quadratic relationship with an optimum at around 50% cover, in line with Sierro et al. (2001). The presence of a dense regrowth in abandoned sites might hinder the bird's hunting activities and again be a direct consequence of fast succession on fertile soils in combination with the on-going changes in land use. The progressive decrease of grazing pressure in loose forest stands and semi-open wooded habitats since World War II has promoted woody stands mainly dominated by deciduous shrubs (Rigling et al. 2006). However, very low levels of shrubs seemed unattractive for Nightjars too, most likely because they provide not enough shelter for roosting (Camacho 2014) and constitute unsuitable habitats for many moth species (Spitzer and Lepg 2012).

Additionally, our results point out the importance of perches (standing and lying dead wood) for Nightjar, corroborating the findings by Wichmann (2004). These structures are used as vantage hunting and singing posts during nighttime, and as daytime roosting sites, respectively. Camouflage among dead bark and branches seems particularly important for daytime roosting sites, again to avoid predation (Jackson 2003; Wichmann 2004; Langston et al. 2007). Improving this habitat feature is easily manageable by either refraining from cutting dead snags or by felling large trees and retaining them in the restored areas.

Moth abundance and biomass were higher in occupied than abandoned sites, with the strongest difference late in the season in July. We observed a general increase in both moth richness and diversity with the advancement of the season, reaching the highest values during the nestling provisioning period (Alexander and Cresswell 1989; Cross et al. 2005). While it is known that Nightjars can forage far away from the nesting site (up to 4km, Evens et al. 2017), enhanced food availability in close proximity to the nesting site most likely reflects the optimal foraging habitat for food-provisioning parents (Evens et al 2018). A potential explanation for reduced prey abundance in aban-

doned and restored Nightjar sites may result from the restoration management itself. Moth abundance usually peaks in old and undisturbed forests with high amounts of native tree species (Summerville and Crist 2004; Spitzer and Lepg 2012; Sharps et al. 2015) where clear-cuts are known to negatively impact moths (Summerville and Crist 2002; Mönkkönen and Mutanen 2003; Summerville 2013; Fedrowitz et al. 2014).

Drawing on these results, we suggest that the long-term persistence of the Swiss Nightjar population relies on open and semi-open forests with a high abundance of moth, this result being in line with previous studies (eg. Sierro et al. 2001; Sharps et al. 2015; English et al. 2017). Most importantly, Nightjar habitat restoration should focus on creating semi-open forest stands on poor, fairly mineral substrates with a poor "succession potential", i.e. with a low regeneration speed of shrubs. A wooded matrix that incorporates a network of smaller clear-cuts that retain heterogeneous vegetation layers would increase the amount of forest edges, which appear to be crucial for Nightjar preservation (Langston et al. 2007; Sharps et al. 2015). Keeping a few old dominating trees, some snags and lying dead wood will further guarantee sufficient availability of perches and daytime roosts. Such a heterogeneous matrix should provide a suitable habitat for the Nightjar and its insectivorous prey. The long-term persistence of an optimal habitat matrix, resembling a dynamic succession stage, is challenging but could be achieved by controlled grazing with highland cattle and goats, as proposed by Sharps et al. (2015) thereby repressing regrowth on lower vegetation strata and creating small-scale disturbances that should positively affect biodiversity in general. More studies investigating the fine-scaled foraging behaviour (Evens et al. 2017) are needed in order to fully understand the species habitat requirements in an inner-alpine habitat context.

AUTHOR CONTRIBUTION

Designed and wrote the manuscript: NW, PK, RA, AJ.

Authors	Contribution	ACI
NW	0.65	5.571
PK	0.05	0.158
RA	0.05	0.158
AJ	0.25	1.000

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Supplementary material 1

Site and moth data

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Data type: species data

Explanation note: Details about the study sites and moths.

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Link: https://doi.org/10.3897/rethinkingecology.3.29338.suppl1